THE EFFECT OF TEMPERATURE ON LINKAGE IN THE SECOND CHROMOSOME OF DROSOPHILA

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Some recent data have shown that certain influences affect the percentage of crossing over. Bridges[1] (1915) noted that the age of the mother altered the result in the second chromosome, and Sturtevant[2] (1917) has recently discovered no less than three definite Mendelian factors which influence the strength of linkage in parts of the second and of the third chromosomes. For two years I have been studying the effect of changes in the environment on the percentage of crossing over in *Drosophila melanogaster* (*ampelophila*). It has been found that very striking effects are produced by differences in temperature for the second chromosome. A full report of this work will appear in a forthcoming number of the *Journal of Experimental Zoölogy.*

Tests of the effect of temperature on the percentage of crossing over were made in the following way. Virgin females from the stock collected originally at Falmouth, Mass., were mated to males homozygous for the second chromosome factors for black body color, purple eyes and curved wings. The pairs were placed successively in two or more sets of bottles for three or four days each. The bottles of the first set were kept at room temperature—about 22°C—and each of the other sets at one of the temperatures to be tested. The normal females heterozygous for black purple curved which hatched from each set were then back crossed to males of the original mutant stock and the offspring allowed to hatch at room temperature. The offspring (F_2) of the back cross show the genetic constitution of the (F_1) eggs, and enable one to calculate the percentage of crossing over between black and purple, and purple and curved. The percentages for the shorter region—black to purple—from a number of experiments involving more than 35,000 flies are shown in the curve given in figure 1. The value at 22°C is the average of the controls for all of the different sets. At lower and higher temperatures—5°C. and 35°C.—no fertile offspring hatched.

The curve is of considerable interest since it shows that both high and low temperatures produce an *increase* in the percentage of crossing over, i.e., a reduction in the strength of linkage. It is plain that the process does not follow van't Hoff's law, as do most physiological processes.[3] The phenomenon therefore involves apparently some change in the physical state of the colloidal substratum of the cells.

Further investigation has demonstrated that the increase in the percentage of crossing over due to high or low temperature applied during the development of the female parent is maintained for only six or seven days after she begins to lay. At the end of this period the percentage drops to the same level as the control. It has also been found that the high or low temperature can be applied to adult females with similar results. After the flies are exposed to the new temperature, an interval elapses during which 225 to 275 eggs are laid which do not show the effect of the new temperature. The percentage then jumps suddenly to the high point where it remains for approximately the length of time of the exposure. A curve illustrating this point is shown in figure 2. The mothers of both series were sisters hatched at room temperature.

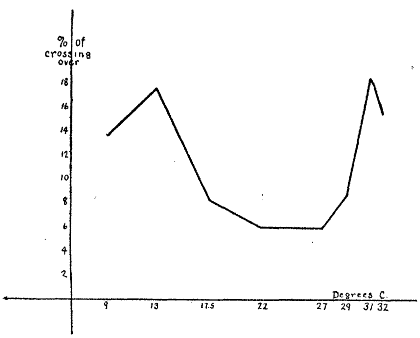

FIG. 1

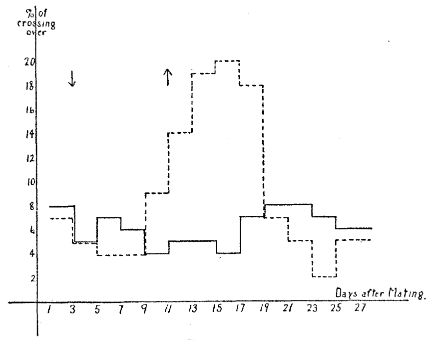

FIG. 2

They were mated and placed in phials which were changed regularly at two day intervals. From the third to the eleventh day the pairs of one series were exposed to a temperature of 31.5°C while the others were continued at room temperature. The percentage of crossing over for the black to purple region is shown in the curve. After an interval of eight days following the beginning of the treatment (i.e., beginning on the same day that the flies were returned to normal temperature) the treated series showed an increase of more than 100% in the amount of crossing over among their offspring. This high ratio was maintained for eight days, after which it returned at once to the control value.

The facts apparently indicate that temperature affects the amount of crossing over at a definite stage in the oogenesis. Exposures to high temperatures for one, two or four day periods make it appear that a consecutive exposure of nearly two days is required to produce any effect at all. Cytological examination has shown that shortly after hatching about 140 eggs have usually passed the last oogonial division. Controls show that eggs are laid at the rate of about 50 a day or 100

in two days. This number of eggs therefore has not received the exposure necessary to produce the change in crossing over. The culmination of the two days exposure is to be expected in those eggs so situated that 125 to 175 eggs will be laid before them. Such an interpretation makes it extremely likely that the change in the amount of crossing over is finally affected in the earliest oocytes, that is, at the beginning of the growth period. The above evidence on the time of applying the new temperature and the time when the change in crossing over occurs, suggests that the crossing over process takes place in the stage when the chromosomes of Drosophila are known to be finely drawn out threads.

The decrease in the strength of linkage caused by temperature in no way weakens the chromosome interpretation of linkage. It rather adds to it considerable support, for it localizes the process of crossing over at a period in oogenesis when twisting between homologous threads seems possible. The evidence positively establishes the fact that crossing over does not take place during the early oogonial divisions, and makes it extremely improbable that it occurs at so late a stage in the growth period as the thick thread stage favored by Janssens as the chiasmatype.

[1] Bridges, C. B., *J. Exp. Zoöl., Wistar Inst., Philadelphia*, **19**, No. 1, July, 1915.
[2] Sturtevant, A. H., these PROCEEDINGS, **3**, 1917, (555–558).
[3] Cf. Snyder, C. D., *Amer. J. Physiol.*, **22**, 1908, (309).

GENETIC FACTORS AFFECTING THE STRENGTH OF LINKAGE IN DROSOPHILA

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In September, 1913, a wild female Drosophila of a stock from Liverpool, Nova Scotia, was crossed to a male bearing the second chromosome mutant characters vestigial and speck. A single daughter of this mating was tested, and gave no crossovers among 99 offspring, though vestigial and speck usually show about 37% crossing over. This strain has since been bred in very large numbers, and the experiments are being continued; but it has seemed advisable to report briefly on some of the results obtained.[1]

It has become clear that the original result was due to something in the second chromosome derived from the Nova Scotia female. Two of her granddaughters and all of her later descendants that were known, from linkage, to have received the second chromosome in question gave